SEABIRD PATCHINESS IN TROPICAL OCEANIC WATERS: THE INFLUENCE OF *SARGASSUM* "REEFS"

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ABSTRACT.—The relationships of seabirds to the holopelagic macroalga *Sargassum* were studied during a 2-yr survey in the South Atlantic Bight off the southeastern United States. Seabirds were significantly more abundant in waters with large (>5 m^2) patches of the alga, and mean avian density was 32–43 times greater in waters where *Sargassum* was present than in adjacent waters without the alga. Seabirds aggregate at *Sargassum* patches formed by Langmuir circulation, convergence fronts, Gulf Stream eddies, and Gulf Stream warm core rings. Twenty-three seabird species foraged at *Sargassum*. Significantly more than 50% of White-tailed Tropicbirds (*Phaethon lepturus*), Masked Boobies (*Sula dactylatra*), and Bridled Terns (*Sterna anaethetus*) were observed at algal patches. Species that use aerial-dipping and plunge-diving foraging behaviors displayed the greatest affinity for *Sargassum*. Large-bodied seabirds (large shearwaters, tropicbirds, and boobies) generally were found at large patches, while small-bodied species (phalaropes and *Puffinus lherminieri*) occurred at smaller patches. The seasonal abundance of the pelagic Bridled Tern corresponded to seasonal variation in *Sargassum* abundance. Most seabirds associated with *Sargassum* for foraging, but Bridled and Black terns (*Chlidonias niger*) also used large algal mats for roost sites. The highly localized biomass of the pelagic *Sargassum* community and its associated motile macrofauna (zooplankton and fish) may allow seabirds to forage efficiently for prey in the oligotrophic surface waters of tropical marine environments. The patchy occurrence of *Sargassum* "reefs" may explain part of the local and mesoscale variation in seabird distribution and abundance in portions of the western North Atlantic Ocean. *Received 19 November 1984, accepted 21 August 1985.*

PATCHINESS in seabird distribution has been little studied, due in part to the difficulty of sampling quantitatively at small scales (Bailey and Bourne 1972, Devillers 1978). The patchy distribution and abundance of seabirds may arise from local concentrations of prey (Brown 1980), or from social interactions critical for successful foraging (Bailey and Bourne 1972, Schneider 1982, Duffy 1983). Interspecific differences in the breeding ecology of seabirds also may affect the patches used for feeding (Erwin 1977). Variability in the physical marine environment of seabirds may indirectly influence the patchiness of prey (Ashmole 1971). Physical features governing seabird patchiness at one scale may account for much of the temporal and spatial variation in seabird patchiness at larger and smaller time/space scales (Haney and McGillivary 1985a).

Seabird patchiness occurs in tropical and subtropical oceans (Haney and McGillivary 1985a, b), characterized by their seasonally stable water masses. The permanent thermocline prevents widespread vertical enrichment of the euphotic zone by nutrient-rich deeper waters, and little variation in primary productivity occurs as a result (Russell-Hunter 1970). Because the food available to higher trophic groups is limited, any factor that elevates the food biomass within this oligotrophic system may be expected to affect seabird distribution and abundance.

The *Sargassum* community and associated fauna are one example of locally elevated biomass in the nutrient-poor waters of the North Atlantic Ocean. Both *Sargassum natans* and *S. fluitans* are widely distributed, holopelagic macroalgae and are restricted to the ocean surface, where gas-filled bladder floats maintain their buoyancy (Parr 1939). The animals inhabiting *Sargassum* have been characterized as a "displaced benthos" (Hedgpeth 1957). Because most of the fauna are derived from populations of littoral genera and species, the fauna and flora together form a pseudobenthic or "reef" habitat surrounded by the pelagic ecosystem (Adams 1960, Weis 1968, Dooley 1972, Fletemeyer 1978, Carr and Meylan 1980, Kracht and Tesch 1981, Bulter et al. 1983).

Although several seabird species have been

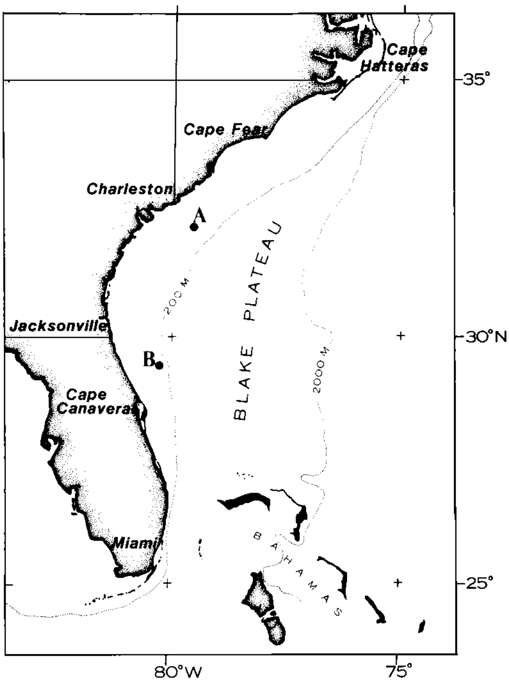

Fig. 1. The South Atlantic Bight with continental shelf (0-200 m) and slope (201-2,000 m) domains where seabird-*Sargassum* associations were studied, 1982-1984. Abundance counts of seabirds associated with *Sargassum* were made at a Gulf Stream eddy (location A) and convergence front (location B).

reported at *Sargassum* or other macroalgae (Bent 1927, Scott 1959, Duncan and Harvard 1980, Rowlett 1980), the possible significance of the *Sargassum* community to seabirds in the western North Atlantic Ocean has not been examined. In this paper I relate interactions of seabirds off the southeastern United States with *Sargassum* and its associated fauna. The following questions were raised in regard to seabird-*Sargassum* associations: (1) Is seabird abundance greater near *Sargassum* patches? (2) Do seabirds aggregate at *Sargassum* patches formed by the various oceanographic features that coalesce the alga? (3) Do seabird species differ in their affinity for *Sargassum*? (4) What are the alga's potential and realized attractions for seabirds?

Study Area and Methods

Most data were gathered in the South Atlantic Bight off the southeastern United States (Fig. 1). The continental shelf consists of three water masses or domains subdivided at the 20-, 40-, and 200-m isobaths (Atkinson et al. 1983). These shelf waters are heavily influenced by the proximity of a strong, persistent western boundary current, the Gulf Stream. The shelf is broad (120 km off Georgia), shallow, and has a relatively shallow shelf break beginning at the 50-75-m isobath. The outer shelf responds mainly to Gulf Stream variations occurring on time scales of 2-14 days (Lee et al. 1981). Variations of the western frontal boundary of the Gulf Stream occur as stable and quasistable waves (meanders) and as unstable waves (frontal eddies) (Pietrafesa and Janowitz 1980). Because the Gulf Stream generally follows the outer shelf edge (ca. 200 m depth) as it flows north, most of the physical and biological effects occur in the outer shelf and upper slope domains (40-400 m).

Seabird surveys were conducted aboard research ships in the South Atlantic Bight from 1982 to 1984. Counts of seabirds were made from vessels cruising at 6-10 knots, using a 15-min count period (Haney and McGillivary 1985b) and 300-m band transect (Tasker et al. 1984). A fixed-interval rangefinder was used to estimate band width and adjust for observation height (Heinemann 1981). Bias was minimized by excluding all birds flying into the count zone from the stern and by using a single observer to record more than 90% of the counts. No counts were made during the few occasions vessels were trawling for or handling fish. Nine-power binoculars were used for detecting seabirds and *Sargassum*.

Most counts ($n = 1{,}880$) were made between 29° and 32°N in the central part of the bight known as the Georgia Embayment. Data were collected monthly on at least one cruise. Observations came from each season (quarter) in inner shelf (0-20 m), middle shelf (21-40 m), outer shelf (41-200 m), and upper continental slope (200^+ m) domains. In addition, one cruise (14 days, 208 counts) was made in August and September 1984 on a transect from Boothbay Harbor, Maine to a location southeast of Bermuda (30°03'N, 63°47'W).

Data recorded during each count included species and number observed, foraging/feeding associations, date, latitude and longitude, heading of ship and birds, ship speed, time of day, visibility, sea height, wind speed and direction, depth, and sea surface temperature (SST). On some cruises, onboard instrumentation allowed continuous recording of depth, SST, salinity, and chlorophyll-*a* fluorescence. During counts, the presence or absence of *Sargassum* was noted, the patch size estimated, and the behavior (resting or foraging) of any accompanying seabirds recorded. Only those individuals foraging, feeding, or resting at *Sargassum* patches were considered associated with the alga. For surface-feeding species (shearwaters, storm-petrels, phalaropes), association was defined as sitting on the water surface within 3 m of *Sargassum* and exhibiting foraging behavior (picking at the surface or submerging). Aerial-foraging/feeding species (tropicbirds, boobies, jaegers, gulls, terns) were considered associated with *Sargas-*

TABLE 1. Relative abundance of seabird species aggregated at *Sargassum* patches and comparison of densities in *Sargassum*-present and *Sargassum*-absent counts.[a]

	n	Percentage of total n	*Sargassum*-present density (km^{-2})	*Sargassum*-absent density (km^{-2})
Counts made at warm filament of Gulf Stream eddy				
Cory's Shearwater	10	34	1.1	0.0
Audubon's Shearwater	1	3.5	0.1	0.1
Masked Booby*	1	3.5	0.1	0.0
Royal Tern	1	3.5	0.1	0.0
Bridled Tern*	16	55	1.8	0.0
Total	29	99.5[b]	3.2	0.1
Counts made at Gulf Stream convergence front				
Wilson's Storm-Petrel	10	16.5	1.4	0.0
Red-necked Phalarope	20	33	2.9	0.0
Common Tern	2	3	0.3	0.0
Least Tern	1	2	0.1	0.0
Bridled Tern*	20	33	2.9	0.2
Black Tern	7	12	1.0	0.0
Total	60	99.5[b]	8.6	0.2

[a] Species marked with an asterisk are those in which more than 50% of the total individuals observed were associated with *Sargassum*.
[b] Total less than 100% due to rounding error.

sum when they were observed foraging within 10 m of or resting on the alga. These definitions of association were used to minimize recording spurious co-occurrences of *Sargassum* and seabirds.

Physical processes influencing *Sargassum* distribution were identified by field observations (Langmuir windrows and some convergence fronts; Fig. 2), by ship-board instrumentation, or by consulting Gulf Stream System Flow Charts (National Oceanic and Atmospheric Administration, Miami, Florida). Gulf Stream charts from November 1982 through October 1984 ($n = 234$) summarized the thermal and circulation regimes in the study area at 2-3-day intervals. These were used to identify Gulf Stream eddies and warm core rings.

RESULTS

SEABIRD ABUNDANCE AND *SARGASSUM*

Seabird abundance in *Sargassum*-present counts averaged 32-43 times higher than in counts without the alga (Table 1). On 14 July 1983 a cluster of large *Sargassum* patches was observed coalesced by convergent circulation on the west and south sides of a large Gulf Stream filament eddy on the outer shelf of South Carolina (Fig. 1, location A). Seabird abundance in counts with *Sargassum* at this location averaged significantly higher than in adjacent counts without the alga ($P < 0.01$; Mann-Whitney U-test; $N = 9, 17$; $Z = 2.499$). Density of seabirds averaged for *Sargassum*-present counts was 3.2 birds/km^2 (SD = 3.4, n = 9) compared with 0.1 birds/km^2 (SD = 0.3, n = 17) in counts $\geq$1 km from the alga. Sixty-three percent (n = 29; Table 1) of the individual seabirds observed belonged to species significantly associated with *Sargassum* (Table 2).

Seabird abundance at a convergence front off Florida (5 May 1984; Fig. 1, location B) was compared with seabird abundance in waters without *Sargassum* immediately adjacent to the front. Seabird abundance was again significantly higher in the counts with *Sargassum* present ($P < 0.01$; Mann-Whitney U-test; $N = 7, 6$; $Z = 2.93$). Seabird density averaged 8.6 birds/km^2 (SD = 7.4, n = 7) in *Sargassum*-present counts vs. 0.2 birds/km^2 (SD = 0.4, n = 6) in counts $\geq$1 km from the alga. Of the total individuals (n = 60) observed, 33% belonged to species significantly associated with the alga (Tables 1 and 2).

INFLUENCE OF *SARGASSUM* PATCH SIZE

Sargassum normally occurs in clumps 10-50 cm in diameter, lying in the direction of the wind in rows 20-50 m apart (Winge 1923, Parr 1939). Because of the buoyancy of the alga, however, larger rafts or patches of *Sargassum* accumulate at oceanographic features that co-

TABLE 2. Contingency table of seabirds associated with *Sargassum*.[a]

	White-tailed Tropicbird	Red-billed Tropic-bird	Masked Booby	Brown Booby	Bridled Tern
Sargassum present					
No. of individuals	10	1	9	2	298
No. of occurrences	10	1	9	2	87
Sargassum absent					
No. of individuals	2	0	2	0	22
No. of occurrences	2	0	2	0	12
Chi-square					
Individuals	5.33	1.0	4.45	2.0	263.86
Occurrences	5.33	1.0	4.45	2.0	56.82
Probability of significance[b]					
Individuals	<0.01	NS	<0.025	NS	<0.005
Occurrences	<0.01	NS	<0.025	NS	<0.005

[a] Number of individuals and occurrences for species in which more than 50% of total numbers in all counts were associated with *Sargassum*.
[b] Pearson's test for homogeneity.

alesce the alga by convergent circulation (Butler et al. 1983). These features vary in size (cf. Fig. 2; Stommel 1963, Haury et al. 1978), and patches formed by each feature may be used by seabirds (Table 3).

Langmuir windrows.—Langmuir circulation (Fig. 2a) is the result of wind-induced helical vortices in surface waters (Langmuir 1938, Faller and Woodcock 1964, Craik and Leibovich 1978, Faller 1978, Leibovich and Paolucci 1980). The patch sizes of *Sargassum* observed at Langmuir windrows during this study were less than 5 m^2. Although the windrows were often very long (0.5–1.0 km), considerable spacing occurred between adjacent patches within the windrows.

Density estimates of seabirds at the small-scale Langmuir windrows were not possible due to count design. However, 10 seabird species were observed foraging at patches formed by this circulation type (Table 3). Audubon's Shearwaters (*Puffinus lherminieri*), phalaropes, and Common Terns (*Sterna hirundo*) foraging near *Sargassum* showed a greater affinity for small patches arising from Langmuir circulation (Table 4). Forty-one percent ($n = 158$) of all *Sargassum*-associated Audubon's Shearwaters foraged at small patches. Ninety percent of Red-necked Phalaropes (*Phalaropus lobatus*; $n = 33$) and 88% of all phalaropes ($n = 68$) observed with *Sargassum* occurred at or next to small patches.

Convergence fronts.—*Sargassum* frequently occurs at boundaries between two water masses of contrasting densities (Butler et al. 1983). Patches of *Sargassum* coalesce at thermal fronts, where colder, denser water sinks beneath warmer, less-dense water (Fig. 2b). Such patches may exceed 5 m^2 in surface area.

The patch sizes of *Sargassum* at fronts, and at the larger eddies and rings, did not show a distinct increase in size corresponding to these progressively larger features. Rather, all three large-scale features (Fig. 2) contained similar patch sizes of the alga, and it was the total area or extent of coverage among features that varied.

Gulf Stream frontal eddies.—Eddies result from unstable variations of the western wall of the Gulf Stream south of Cape Hatteras, North Carolina (Pietrafesa and Janowitz 1979, Lee et al. 1981, Lee and Atkinson 1983). Eddies flow north along the shelfbreak with the stream and may extend over 100 km in length and 50 km in width. Downwelling or convergence at eddies occurs principally along the western and southern edge of the warm filament (Fig. 2c; Pietrafesa and Janowitz 1980). Patches of *Sargassum* exceeding 1 ha were found on occasion at these locations.

Gulf Stream warm core rings.—Gulf Stream warm core rings are circulating bodies of water about 100 km in diameter that occur north of Cape Hatteras, North Carolina (Fig. 2c). Warm core rings transport less-productive Sargasso Sea water into slope waters between the Gulf Stream and the northeast U.S. continental shelf (Leetma 1977, Watts and Olson 1978). Large rafts of *Sargassum* are carried shoreward into slope waters with the rings (Butler et al. 1983, pers. obs.).

Thirteen of the 23 seabird species occurred only at the large (>5 m^2) patches in fronts, eddies, or rings (Table 3). Although Bridled and Black terns occurred at both patch sizes, 95% (n = 298) of all Bridled and 98% (n = 173) of all Black terns were associated with large patches. Eighty-eight percent (n = 1,473) of all *Sargassum*-associated birds were found at large patches formed by fronts, eddies, or rings (Table 3).

Seabird body size and patch size.—When the numbers of individual seabirds per occurrence at small (<5 m^2) and large (>5 m^2) *Sargassum* patches were compared, interspecific differences were detected (Table 4). Only species in which 10 or more individuals associated with *Sargassum* were used to calculate patch-size affinities. An index of affinity for large patches was developed using a ratio based on the difference in the number of individuals per occurrence at large (F_2) and small (F_1) patches [$(F_2 - F_1)/F_2$; Table 4]. Larger-bodied seabirds generally showed a positive affinity for large patches, while some small-bodied seabirds showed a strong negative affinity for large patches (Table 4, Fig. 3). The relationship between seabird body size and affinity for large patches was positive (r = 0.429 for length and 0.317 for mass), but not significant using all data points (Fig. 3).

Species ≥40 cm in length and 0.5 kg in weight showed a preference for large *Sargassum* patches. All Cory's Shearwaters (*Calonectris diomedea*), White-tailed Tropicbirds, and Masked Boobies were seen at large rafts of *Sargassum* at fronts, Gulf Stream eddies, or warm core rings. The affinities of intermediate-size seabirds (30–40 cm and <0.5 kg) were less clear. Species 30 cm or smaller (except Black Tern) generally showed an affinity for small algal patches.

SEABIRD ATTRACTION TO *SARGASSUM*

Seabirds with the greatest affinities for *Sargassum* were aerial-dipping and plunge-diving species (Table 5) that feed primarily on fish (diets reviewed by Clapp et al. 1982, 1983). The diets of these species include juvenile jacks (Carangidae) and flying fish (Exocoetidae), both of which are abundant in *Sargassum* (Dooley 1972). These fish aggregations represent localized and elevated seabird forage in otherwise oligotrophic surface waters.

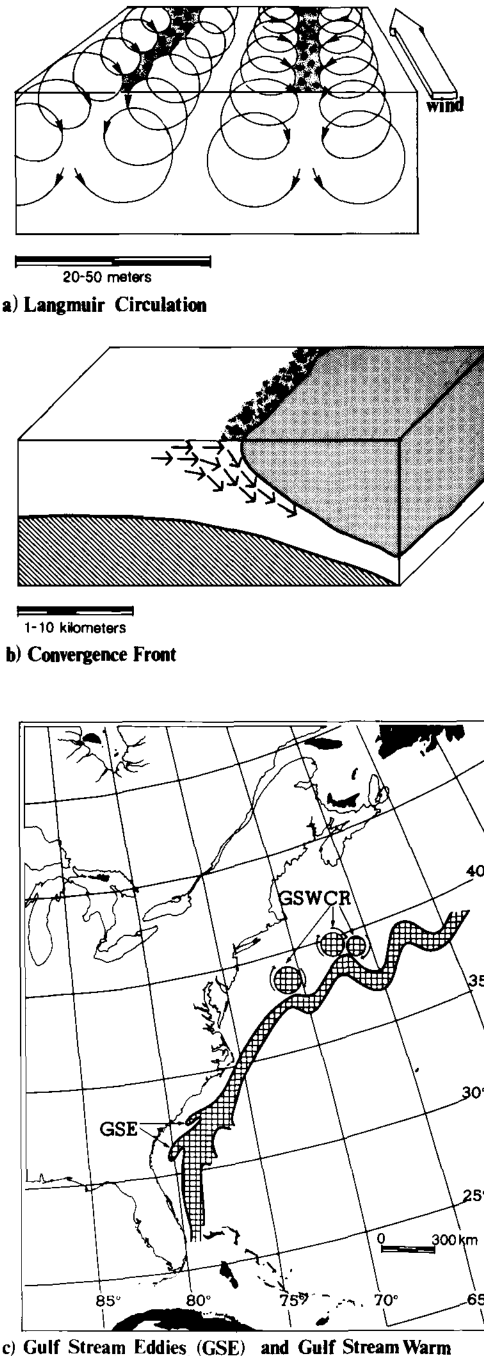

Fig. 2. Fine (a), coarse (b), and mesoscale (c) circulation influencing the spatial distribution of *Sargassum* in the western North Atlantic Ocean (Haury et al. 1978, Butler et al. 1983). Patchiness in algal distribution is illustrated in (a) and (b). Seabirds associated with algal patches formed by each feature are listed in Table 3.

TABLE 3. Total numbers of individuals (N_1) and occurrences (N_2) of seabird species foraging or resting at *Sargassum*. Data are subdivided to reveal associations at each of four circulation events that coalesce *Sargassum* above mean patch size.

Species	Langmuir circulation		Convergence front		Gulf Stream eddy		Gulf Stream ring		Total	
	N_1	N_2	N_1	N_2	N_1	N_2	N_1	N_2	N_1	N_2
Black-capped Petrel (*Pterodroma hasitata*)	13	4	3	2	70	11	—	—	86	27
Cory's Shearwater (*Calonectris diomedea*)	—	—	40	18	199	19	4	1	243	38
Greater Shearwater (*Puffinus gravis*)	—	—	2	1	1	1	1	1	4	3
Audubon's Shearwater (*Puffinus lherminieri*)	65	4	17	13	55	14	21	1	158	32
Wilson's Storm-Petrel (*Oceanites oceanicus*)	6	4	13	7	32	17	280	1	331	29
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	—	—	2	2	1	1	32	1	35	12
Band-rumped Storm-Petrel (*Oceanodroma castro*)	1	1	—	—	3	2	—	—	4	3
White-tailed Tropicbird (*Phaethon lepturus*)	—	—	8	8	2	2	—	—	10	10
Red-billed Tropicbird (*Phaethon aethereus*)	—	—	1	1	—	—	—	—	1	1
Masked Booby (*Sula dactylatra*)	—	—	2	2	7	7	—	—	9	9
Brown Booby (*Sula leucogaster*)	—	—	1	1	1	1	—	—	2	2
Red-necked Phalarope (*Phalaropus lobatus*)	30	7	1	1	2	2	—	—	33	10
Red Phalarope (*Phalaropus fulicaria*)	—	—	—	—	2	2	—	—	2	2
Phalarope sp. (*Phalaropus* sp.)	31	2	2	2	—	—	—	—	33	4
Pomarine Jaeger (*Stercorarius pomarinus*)	2	2	—	—	2	2	—	—	4	4
Parasitic Jaeger (*Stercorarius parasiticus*)	—	—	1	1	—	—	—	—	1	1
Jaeger sp. (*Stercorarius* sp.)	—	—	1	1	3	2	1	1	5	4
Herring Gull (*Larus argentatus*)	—	—	12	5	—	—	—	—	12	5
Royal Tern (*Sterna maxima*)	—	—	1	1	1	1	—	—	2	2
Common Tern (*Sterna hirundo*)	9	1	—	—	4	1	—	—	13	2
Arctic Tern (*Sterna paradisaea*)	—	—	—	—	8	4	—	—	8	4
"Comic" Tern (*Sterna* sp.)	—	—	—	—	15	7	—	—	15	7
Least Tern (*Sterna antillarum*)	—	—	2	2	—	—	—	—	2	2
Bridled Tern (*Sterna anaethetus*)	5	6	121	37	162	33	—	—	298	76
Sooty Tern (*Sterna fuscata*)	—	—	1	1	—	—	—	—	1	1
Black Tern (*Chlidonias niger*)	5	1	131	7	37	10	—	—	173	18
Percentage of total number of birds (n = 1,473) in each circulation feature	12.0		23.8		41.2		23.0			
Number of species at each feature	10		19		19		6			

In addition to foraging habitat, the "solid" substrate of *Sargassum* provided roost sites for pelagic and semipelagic terns (Table 6). Twenty-seven percent of all *Sargassum*-associated Bridled Terns and 71% of all Black Terns were observed either on *Sargassum* or on solid debris within algal patches. Significantly more Black than Bridled terns used large *Sargassum* patches for roost sites ($\chi^2 = 9.53$, $P < 0.005$, df = 1). This may stem from a difference in the social organization of the two species. Bridled Terns seldom occurred in groups of more than 6 individuals, and the mean size of resting groups was small ($\bar{x}$ = 2.15, SD = 1.91, n = 13). Black Terns often occurred in larger groups of 12 or more, and the mean size of resting groups was larger ($\bar{x}$ = 23.75, SD = 20, n = 4). Resting group sizes of the two species differed significantly ($P < 0.05$; Mann-Whitney U-test; N = 4, 13; Z = 2.32).

Seasonal abundance of the Bridled Tern corresponded to seasonal variation in *Sargassum* abundance (Fig. 4). *Sargassum* fluctuates seasonally within the Florida Current (Gulf Stream); low quantities of the alga are present in winter and spring, and large quantities in summer and fall (Dooley 1972). Although Dooley's monthly *Sargassum* abundance figures came from south of the study area defined here, they are characteristic of the South Atlantic Bight north to Cape Hatteras (Butler et al. 1983, D. S. Lee pers. comm.). The monthly abundances of Bridled Terns and *Sargassum* were positively correlated ($r = 0.692$, $P < 0.05$, df = 8; Fig. 4).

DISCUSSION

Species affinities for Sargassum.—Few seabird species occurred exclusively at *Sargassum*. The affinities of seabirds for *Sargassum* within the

TABLE 4. Species variation in the number of individuals/observation foraging at small and large *Sargassum* patches.[a]

Species	Patch size Small (F_1)	Large (F_2)
Black-capped Petrel (BCPE)[b]	3.25	5.65
Cory's Shearwater (COSH)	0.0	6.39
Audubon's Shearwater (AUSH)	16.25	3.32
Wilson's Storm-Petrel (WISP)	1.5	1.87[c]
White-tailed Tropicbird (WTTB)	0.0	1.0
Masked Booby (MABO)	0.0	1.0
Red-necked Phalarope (RNPH)	4.29	1.0
Phalarope sp. (UNPH)	15.5	1.0
Common Tern (COTE)	9.0	4.0
"Comic" Tern (UNTE)	0.0	2.14
Bridled Tern (BRTE)	2.5	4.04
Black Tern (BLTE)	5.0	9.88

[a] Small patches were defined as those induced by Langmuir circulation (<5 m²) and large patches by fronts, eddies, or rings (>5 m²).

[b] Abbreviations for species in Fig. 3.

[c] Wilson's Storm-Petrels at a Gulf Stream warm core ring were excluded in this calculation due to concurrent processes (upwelling) that affected their distribution.

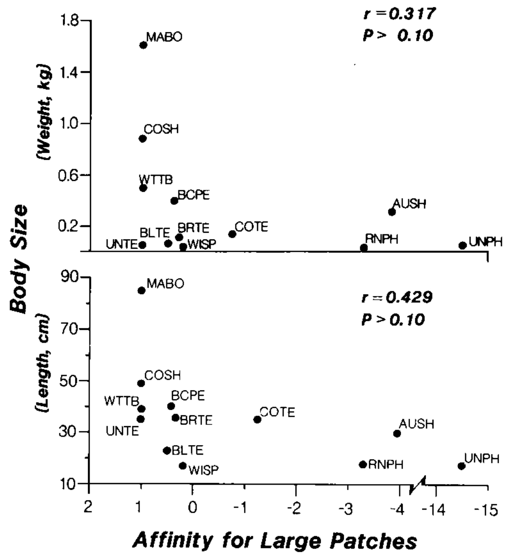

Fig. 3. Relationship of seabird body size to the degree of affinity for large (>5 m²) *Sargassum* patches. Species abbreviations are defined in Table 4.

study area can be perceived as a continuum ranging from species that nearly always associated with the alga to species that rarely did. For three species (White-tailed Tropicbird, Masked Booby, Bridled Tern; Table 2), significantly more than 50% of individuals and occurrences were associated with the alga.

The post- or nonbreeding portion of the Bridled Tern's life history appears most closely linked with *Sargassum.* Duncan and Havard (1980) found all Bridled Terns they observed at *Sargassum* "weed" lines in the northern Gulf of Mexico. This species also displayed the strongest relationship to the alga in the South Atlantic Bight (Table 2). The abundances of Bridled Terns differed between 1983 and 1984 in this region. In 1984, 0.81 terns per observation hour ($n = 76$) were recorded on the outer shelf compared with 1.57 terns per observation hour ($n = 178$) in 1983. Less *Sargassum* was observed in 1984, due either to random variation in encounters between the two years or to an interannual fluctuation in algal abundance (Butler et al. 1983). Both explanations are consistent with the co-occurrence of Bridled Terns and *Sargassum.*

Seasonality in *Sargassum* occurrence may be at least a contributing factor in the seasonal pattern of Bridled Tern abundance in the South Atlantic Bight. This seasonal pattern of Bridled Tern occurrences (Fig. 4; Clapp et al. 1983) is not easily reconciled with the species' breeding cycle alone. Diamond (1976) found that nesting by this species in the Seychelles may occur at any time of the year. The appearance of adult Bridled Terns off the southeastern U.S. coast from mid-April to late June is difficult to ascribe to postbreeding dispersal, particularly when it is during this period that the species nests in the West Indies–Caribbean region (Bent 1921, Watson 1966).

For some seabird species, the degree of association with *Sargassum* was location-dependent. For example, less than 10% of all Black Terns observed shelf-wide were found at *Sargassum.* Most Black Terns accompanied mackerel (Scombridae) and jack (Carangidae) schools in nearshore waters. However, 97% of total individuals ($n = 178$) occurring in the less-productive outer shelf and Gulf Stream waters occurred at *Sargassum.* Phalaropes showed a similar relationship to the alga. The majority of phalaropes observed were found in the middle shelf, where they fed at oceanic fronts that concentrate zooplankton (Haney and McGillivary 1985a, Haney 1985a). In the more pelagic outer shelf and slope domains, 95% ($n = 74$) of phalaropes were *Sargassum*-associated. *Sargassum* may have represented the best available foraging sites for seabirds migrating and foraging over these oligotrophic waters.

TABLE 5. Principal seabird feeding methods of species when associated with *Sargassum*.[a] Terminology is based on Ashmole (1971), Ainley (1977), and Clapp et al. (1982).

Aerial dipping	Plunge diving	Pursuit diving	Surface seizing
Black-capped Petrel	White-tailed Tropicbird*	Audubon's Shearwater	Cory's Shearwater
Wilson's Storm-Petrel	Red-billed Tropicbird*		Greater Shearwater
Leach's Storm-Petrel	Masked Booby*		Red-necked Phalarope
Band-rumped Storm-Petrel	Brown Booby*		Red Phalarope
Bridled Tern*	Royal Tern		Pomarine Jaeger
Sooty Tern	Common Tern		Parasitic Jaeger
Black Tern	Arctic Tern		
	Least Tern		

[a] Species marked with an asterisk are those in which more than 50% of the total individuals observed were associated with *Sargassum*.

The degree of affinity by some seabird species for *Sargassum* could have been underestimated. Audubon's Shearwaters observed close to ships were frequently seen feeding singly at small (<30 cm) clumps of *Sargassum*. Individuals fed by sitting next to the clump, peering underwater with the head submerged, then diving briefly, perhaps to feed on the few filefish that accompany even very small *Sargassum* clumps (pers. obs.). Because small algal clumps were not usually visible beyond 100 m, the affinity of Audubon's Shearwaters for these microscale patches could not be completely evaluated.

The remaining seabird species (Table 3) were rare *Sargassum* associates. Some of these species [e.g. Band-rumped Storm-Petrel (*Oceanodroma castro*), Red-billed Tropicbird (*Phaethon aethereus*), Brown Booby (*Sula leucogaster*)] were rare throughout the study area. Other species [Black-capped Petrel (*Pterodroma hasitata*), storm-petrels, jaegers, gulls, terns; Table 3] were observed more frequently in other foraging modes. Normally kleptoparasitic jaegers, for example, only occasionally fed at *Sargassum*, where they incidentally ingested algal blades when feeding on fish eggs (Haney unpubl. data).

The relationship between seabird species' body size and algal patch size (Table 4, Fig. 3) might be attributed to interspecific exclusion or partitioning, but this seems unlikely because, compared with other foraging modes, *Sargassum*-based feeding/foraging is rare in all but a few species (Tables 2 and 5). Dooley (1972) found a positive correlation between *Sargassum* biomass and the numbers of the two most numerous *Sargassum*-associated fish species. Skin-diving revealed that large fish are found primarily beneath large algal mats (pers. obs.). Large seabirds thus may find the size frequencies of preferred prey only at large patches, and in greater numbers. Smaller seabird species may find their prey more accessible at the small patches that offer more surface area per unit volume.

Ecological significance of Sargassum.—*Sargassum* provides localized and concentrated prey for seabirds in a generally unproductive ma-

TABLE 6. Behavior of tern species at *Sargassum* patches.[a]

	Langmuir circulation		Convergence front		Gulf Stream eddy	
Species	Percentage foraging	Percentage resting	Percentage foraging	Percentage resting	Percentage foraging	Percentage resting
Royal Tern	—	—	100	—	—	100
Common Tern	100	—	—	—	100	—
Arctic Tern	—	—	—	—	100	—
"Comic" Tern	—	—	—	—	100	—
Least Tern	—	—	100	—	—	—
Bridled Tern	60	40	40.5	59.5	99	1
Sooty Tern	—	—	100	—	—	—
Black Tern	100	—	6	94	100	—

[a] Sample sizes given in Table 3.

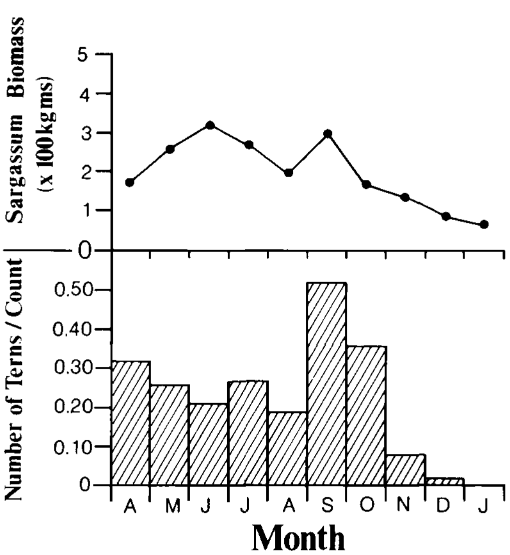

Fig. 4. Comparison of the relative monthly biomass of *Sargassum* to monthly abundance of Bridled Terns on the outer shelf and upper slope (40–400 m) off the southeastern United States. Monthly tern abundances are based on pooled 1983 and 1984 counts.

rine environment. At least 100 species of organisms, mostly invertebrates, compose the *Sargassum* community (Morris and Mogelberg 1973). As many as 54 additional species of fish associate with the alga at some time in their life cycles (Dooley 1972, Bortone et al. 1977). *Sargassum* functions as a nursery for these fishes (Dooley 1972), but algal mats also may attract species seeking temporary shelter from predators (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Helfman 1981). Dooley (1972) found juvenile (10–70 mm) planehead filefish (*Monacanthus hispidus*) to be the most numerous fish in *Sargassum*. Young filefish are not found in open water away from the alga. Audubon's Shearwaters, Black-capped Petrels, and Bridled Terns consume juvenile filefish, often in considerable numbers (Haney unpubl. data).

The motile meiofauna in *Sargassum* consists mainly of cyclopoid and harpacticoid copepods and *Latreutes* shrimp (Butler et al. 1983, Stoner and Greening 1984). Because phalaropes are specialized zooplankton feeders (Dodson and Egger 1980), the association of phalaropes with *Sargassum* may be due to elevated zooplankton abundance relative to adjacent waters. Phalaropes were observed feeding at *Sargassum* clumps, and associations of phalaropes with pelagic macroalgae have been reported elsewhere (Bent 1927, Scott 1959, Rowlett 1980).

Why seabirds use *Sargassum* for roost sites is not entirely clear. Resting on substrates like *Sargassum* may enable terns to conserve energy when not foraging (Table 6). Such substrates may serve as comparatively "dry" sites for resting and preening birds that are migrating long distances. The feathers of the highly pelagic Sooty Tern (*Sterna fuscata*) are said to become soaked, and birds drown when contact with water is prolonged (Clapp et al. 1983: 666). Poor water-resistant properties in Black and Bridled tern plumages may be a factor in the affinity of these species for *Sargassum* roost sites. Individuals of both species were never observed resting on the ocean surface.

Sargassum is but one source or cause of seabird patchiness in the South Atlantic Bight region. Oceanographic features like fronts, eddies, rings, and Langmuir circulation may influence seabird foraging independently of the occurrence of *Sargassum* (cf. Yoder et al. 1981, 1983; Haney 1985b). However, biased associations or spurious relationships between seabirds and *Sargassum* were unlikely to be a factor in this study. Counts and observations of seabirds were not attributed to *Sargassum* when strong evidence existed that an alternate explanation (e.g. upwelling) was the source of attraction, co-occurrences or associations of seabirds and *Sargassum* were listed only when individual birds exhibited feeding or foraging very near the alga, and seabirds were not observed feeding in open water between *Sargassum* patches, which might be expected if they were attracted to the physical feature for some alternative reason.

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